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Unravelling the impact of anthropogenic pressure on plant communities in Mediterranean temporary ponds

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Abstract. Identifying the respective role of environmental, landscape and management factors in explaining the patterns in community composition is an important goal in ecology. Using a set of 32 temporary ponds in northern Morocco we studied the respective importance of local (within the pond) and regional (density of ponds in landscape) factors and the impacts of different land uses on the plant species assemblages, separating pond and terrestrial species. The main hypotheses tested were that (1) species assemblages respond to both local and regional environmental factors, (2) anthropogenic pressure has a negative influence on the number of pond species, and that (3) human activities differ in their impact on pond biodiversity. The results showed that (1) local factors explain most of the variation in plant community composition, and (2) land use impacts the communities through changing local environmental conditions, leading to a loss of typical pond species. Aside from recreation, all other activities (grazing, drainage, agriculture and partial urbanisation) significantly reduced the number of pond species. The conservation strategy for rare pond species should focus on maintaining networks of oligotrophic ponds, while allowing only low-impact activities.

Additional keywords: biodiversity, conservation, disturbance, freshwater.

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Introduction

Mediterranean temporary ponds are endorheic depressions that, due to the Mediterranean climate (hot, dry summers and cool, wet winters), are characterised by alternating dry and flooded phases (Grillas *et al.* 2004). These habitats harbour a high biodiversity, often including rare and endemic species (Grillas *et al.* 2004). Ponds also possess great value in terms of use by the local populations (e.g. water supply for humans, livestock and wildlife, grazing, agriculture, harvest of medicinal plants, etc.) (Rhazi *et al.* 2006). Despite their ecological and socio-economic value, the number and quality of temporary ponds is rapidly declining worldwide (e.g Deil 2005; Zacharias and Zamparas 2010). Due to their small area and shallow depth, these habitats are vulnerable and mostly threatened by the intensification of anthropogenic land uses, especially in agricultural regions (Grillas *et al.* 2004). Diversity, community composition and species distribution patterns in temporary ponds are controlled by complex interactions between various natural and anthropogenic factors (Deil 2005; Rhazi *et al.* 2006). Knowledge concerning the contribution of each of these factors is important to understand biodiversity and species distribution patterns and to develop strategies for conservation and sustainable use of aquatic systems in general (Declerck *et al.* 2006; Mikulyuk *et al.* 2011).

Local factors, such as hydrology, soil characteristics and light availability, are generally the main proximal factors controlling plant communities in temporary ponds (e.g. Casanova and Brock 2000; Deil 2005). The plants typically found in these habitats are adapted to alternating wet and dry phases and to large interannual changes in hydroperiods (timing and duration of flooding) (Zedler 1987; Casanova and Brock 2000). The physico-chemical characteristics of the soil (e.g. particle size, availability of nutrients, soluble minerals and pH) also play an important role in the distribution of species in wetlands (Lathrop 1976; Crowe *et al.* 1994).

Regional factors, such as the density of ponds in the surrounding area, also influence species richness and composition of plant communities in aquatic systems (Mikulyuk *et al.* 2011; Rhazi *et al.* 2012). The communities in ponds operate as metacommunities, in which dispersal between ponds is mediated by several vectors, such as animals, water and wind (Figuerola and Green 2002; Vanschoenwinkel *et al.* 2008).

Human activities often lead to changes in local environmental conditions of ponds (e.g. hydroregime, nutrient levels), as well as in regional factors. The decreasing density of ponds in the landscape increases their isolation, reducing biological connections (Rhazi *et al.* 2012). These changes in local and regional factors are likely to affect plant communities, promoting the growth of terrestrial species with high dispersal rates and plasticity. Conversely, specialised pond species, with limited dispersal rates or more stringent ecological requirements, are likely to be more impacted by such changes (Rhazi *et al.* 2001; Crosslé and Brock 2002). Plant communities of Mediterranean ponds have long been influenced by human activities (Amami 2010). However, an increase in frequency and intensity of these activities may ultimately cause local extinctions and thus reduce the species richness of these habitats (Rhazi *et al.* 2001; Bouahim *et al.* 2010).

From a perspective of sustainable management and conservation of Mediterranean temporary ponds, this study aimed to identify the key factors that determine the richness and composition of plant communities. A set of Moroccan temporary ponds with varying degrees of anthropogenic pressures were used as a model system. The main hypotheses tested were: (1) species richness and community composition respond primarily to local and secondarily to regional environmental factors; (2) anthropogenic pressure has a significant influence on species richness and composition, decreasing the number of specialised pond species; and (3) human activities differ in their impact on pond biodiversity, some of which are compatible with maintaining a high pond biodiversity. To our knowledge, our study is the first to assess the respective role of local, regional and anthropogenic factors on the assemblage of pond and terrestrial plant species in Mediterranean temporary ponds.

Methods

Study site

The study was conducted in the region of Benslimane, situated between Rabat and Casablanca in Western Morocco (Fig. 1). This region is characterised by a semiarid Mediterranean climate with warm winters, an average rainfall of 450 mm per year (mostly in winter) and average minimum and maximum temperatures of 7.5°C and 29.5°C, respectively (Zidane 1990). The underlying rock formation is sandstone–quartzite with hydromorphic soil. The landscape consists mainly of cork oak (*Quercus suber*) forests and crop land (Fig. 1). The region is dotted with numerous temporary ponds, varying in size and depth, covering ~2% of the total surface area of the province

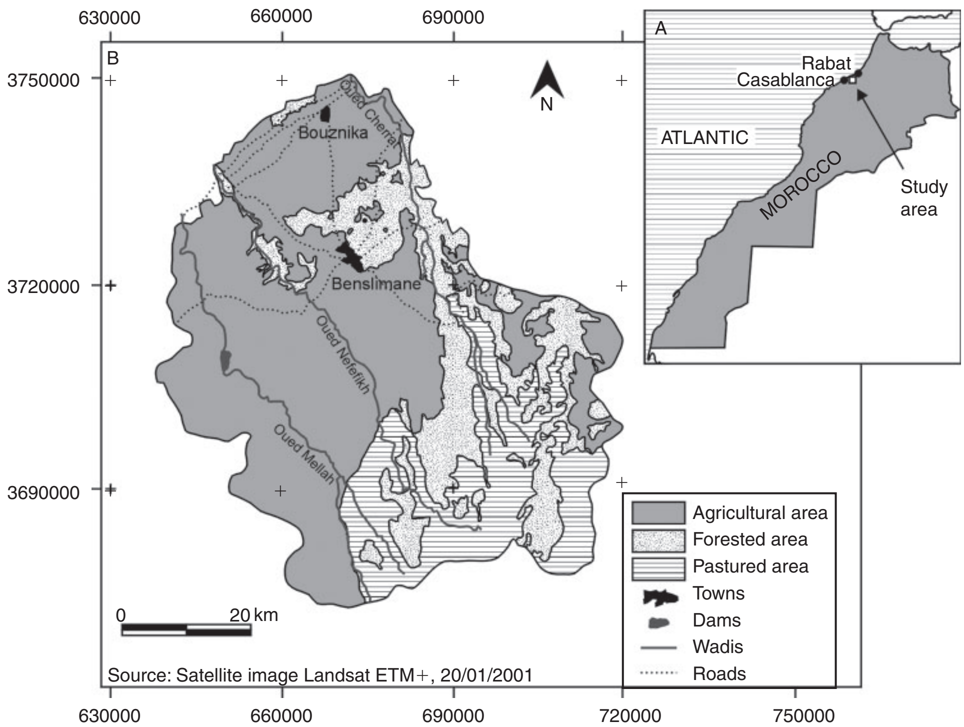

Fig. 1. Location of (*A*) Benslimane province and (*B*) the study area within map of land uses.

(Rhazi *et al.* 2006). These ponds are used for cattle grazing, recreation and water supply and are often totally or partially transformed by agriculture or urbanisation. In this region, a loss of 23% in number and 61% in surface area of ponds was reported over a period of almost 50 years (Rhazi *et al.* 2012).

Plant communities

In total, 111 temporary ponds have been identified in an area of 7300 ha around the town of Benslimane (62 in forest and 49 in agricultural areas). Of these, 32 ponds were selected following a process of random selection stratified by landscape (16 in forested areas, 16 in agricultural areas), size (<1 ha: 13; 1–2 ha: 6; 2–3 ha: 4; 3–4 ha: 4; >4 ha: 5 ponds) and human uses. During two visits, in February and May 2009, a phytosociological survey (Braun-Blanquet 1932) was conducted on plots of 64 m^2. Two plots were surveyed per pond, one at the centre and one at the periphery, in order to have a better description of the vegetation of the pond across the hydrological gradient (Wilson and Keddy 1985). The peripheral site was selected haphazardly, but avoiding any feature that would reduce its representativeness (e.g. presence of rocks, shade of a tree, inconsistent slope). The abundance of each species was calculated as the maximum abundance recorded during the two surveys, considering both plots (centre and periphery).

The vegetation of each pond was characterised by the cumulative species richness (total number of species identified over the two surveys and both plots) of three groups of species: terrestrial, pond and rare species. Pond characteristic species have been defined as aquatic and amphibious wetland species, more or less strictly associated with temporary ponds (Chevassut and Quézel 1956; Médail *et al.* 1998; Rhazi *et al.* 2012). Rare species constitute a subgroup of pond species of conservation interest in Morocco. These are defined by at least one of the following criteria: they are present in fewer than five localities or known from only one or two floristic regions of Morocco (Jahandiez and Maire 1931–1934) or a decline in their populations has been demonstrated (Fennane and Ibn Tattou 1999). Terrestrial species are defined as opportunistic plants, commonly found in forested and agricultural areas surrounding the ponds (Fennane *et al.* 1999, 2007) and which penetrate into the ponds during the dry phase. Total abundances of terrestrial, pond-characteristic and rare species were calculated for each pond as the sum of the species abundances in each category.

Local factors

During each vegetation survey maximum water depth was measured in each of the 32 ponds. Pond surface was measured using a GPS in the field. Two sediment samples (top 10 cm) were taken respectively at the centre and the periphery of each pond (close to the vegetation survey plots) to determine several soil characteristics. Each sample comprised 10 subsamples (4 cm diameter) randomly taken and mixed manually. Particle size was assessed using the 'Bouyoucos' method (Black *et al.* 1985). The pH of the sediment was measured using a pH meter in a suspension of fine soil with a soil/distilled water weight ratio of 1 : 2.5. The content of soluble ions ('salinity') of the sediment was measured as electrical conductivity (conductivity meter Philipps PR 9801) of a soil/double-distilled water solution with a weight ratio of 1 : 5, after stirring for 1 h (150 revolutions min^{-1}) (Black *et al.* 1985). Standard protocols were followed for the measurement of organic matter, phosphorus (Olsen P) and total nitrogen (Kjeldahl N) in sediment (Page *et al.* 1984).

Regional factors

The density of ponds around each of the studied ponds was calculated to assess the potential degree of connectivity between ponds within the landscape. A Geographic Information System (GIS) was used to quantify the number of ponds present in increasing radii (100, 200, 300, 400, 500, 600, 1000, 1500 m) around each of the ponds.

Anthropogenic factors

Different uses were identified for each of the studied ponds during field visits and interviews with local people living close to these ponds. These uses were classified in nine categories: cattle grazing, harvesting medicinal plants, drying (e.g. water pumping, drainage), recreation, extraction of sediment, domestic activities (e.g. washing clothes), crop cultivation (on the margins or within the pond), filling in and urbanisation (Table 1). An anthropogenic pressure index (API) was assigned to each pond to quantify the degree to which the pond is likely to be negatively affected by human impact (Schröter *et al.* 2004). Following the approach adopted by Schmoldt and Peterson (2000) and O'Connor and Kuyler (2009), indices of anthropogenic impact (IAi) were assigned to each of the different uses by consensus among a panel of specialists in temporary pond ecology and wetland socio-economy (see Authors and Acknowledgements) (Table 1). Thus, each pond was attributed a suite of indices of anthropogenic impact corresponding to the different uses. The API of each pond was then calculated as the sum of these indices of anthropogenic impacts: $API = \sum IA_i$.

Data analysis

Multivariate analyses were performed using R (2.15.1) (R Development Core Team 2008), while univariate analyses were performed with STATISTICA 10 (Statsoft, Tulsa, OK). The relative influence of local environmental factors (soil characteristics, maximum water depth and surface of ponds), regional factors (density of ponds in the surrounding area) and anthropogenic factors (API) on the plant community composition was analysed using multivariate statistics performed on species abundances. Therefore, several matrices were created. First, two species data matrices were created with species abundances as columns and ponds as rows. This was done separately for the terrestrial species and the pond-characteristic species, as they were analysed separately. Second, three matrices of explanatory variables were created: an environmental matrix containing all local factors, a regional factors matrix and an anthropogenic factors matrix. All analyses were performed separately for the terrestrial and pond-characteristic species in order to test the unique and common variation of these three groups of variables on the different groups of species. We opted for redundancy analyses (RDA), rather than canonical correspondence analysis, since detrended canonical correspondence analyses indicated a dominance of linear gradients (Lepš and Šmilauer 2003). First, RDA-based forward-selection procedures were used to determine significant explanatory variables within each of the three

Table 1. Anthropogenic impact of the different identified land uses (AI_i) and their frequency of occurrence in the 32 ponds studied

Land use	Impact	AI_i	Frequency
None	No impact	0	8
Recreation	Trampling and solid pollution (mostly during dry season).	0.5	4
Grazing (pasture)	Low impact on specific floristic species richness and abundance (Bouahim *et al.* 2010).	1	24
Medicinal plant harvest	Low impact on vegetation (limited number of harvested plants) (field observation 2007–09).	1	1
Domestic activities (e.g. washing clothes)	Eutrophication of the environment (Rhazi *et al.* 2001).	3	1
Extraction of materials (e.g. rock, sediment)	Change in hydrological regime and loss of plant biodiversity by destroying the seed bank (Rhazi *et al.* 2006).	4	1
Agriculture	Loss of ecosystem functions and plant biodiversity through disturbance and input of herbicides (Anderson and Vondracek 1999; Rhazi *et al.* 2001, 2006; García-Muñoz *et al.* 2009).	4	8
Filling	Change in hydrological regime and loss of pond functions and biodiversity (Rhazi *et al.* 2006).	4	1
Drying (e.g. drainage, pumping, *Eucalyptus* plantation)	Decrease of water height and flood duration in the ponds with decrease of the most aquatic species and enhanced encroachment of opportunistic terrestrials (Rhazi *et al.* 2006).	4	9
Urbanisation (e.g. hotels, sport fields)	Irreversible destruction of ponds, loss of aquatic ecosystem functions and biodiversity (UICN 2000).	5	5

categories (local, regional or anthropogenic), both for the pond-characteristic species and for the terrestrial species. Subsequently, retaining only these significant explanatory variables, RDA-based variation partitioning was used to compare the contribution of each category of variables alone or together with other variables (Borcard *et al.* 1992). The statistical significance of the analysis was assessed by Monte Carlo permutation tests ($n = 999$). To visualise the relations between the explanatory variables and community composition, Principal Component Analysis (PCA) was used with the selected (i.e. significant in the RDAs with forward selection) local, regional or anthropogenic factors plotted as supplementary variables. Rarely encountered species (33 species that occurred in only one or two ponds) were not taken into account in these analyses as they may have a disproportionate impact on the analyses. Species richness per pond was not normally distributed, so univariate Spearman regressions were performed to assess the relationship between species richness per pond (including the rarely encountered species) and the selected significant explanatory local, regional and anthropogenic factors.

Additionally, a separate RDA was used to determine the impact of the different land uses on the assemblage of the pond-characteristic species. For this, an additional land-use matrix was created, with the presence/absence of the different land uses as columns and ponds as rows. Only land uses identified in more than two ponds were considered for this analysis (i.e. recreation, grazing, drainage, partial urbanisation and cultivation). The influence of each land use on the richness and abundance of pond characteristic and rare species was also tested using one-way ANOVA.

Results

The year of the study (2009) was very wet, with a total annual rainfall of 724 mm (160% of the average over the last 30 years). In the 32 ponds, a total of 200 species were recorded (65% annuals and 35% perennials; 64% terrestrial species and 36% pond-characteristic species). Among the pond species, eight rare species for Morocco were found: *Elatine alsinastrum*, *Elatine brochonii*, *Exaculum pusillum*, *Helosciadium inundatum*, *Isoetes velata*, *Lythrum thymifolia*, *Myriophyllum alterniflorum* and *Pilularia minuta*.

Effects of local, regional and anthropogenic factors

Some of the explanatory variables used in the analyses were significantly correlated (Appendix 1). One of the most important correlations is that the 'non-use' of ponds was strictly negatively correlated with grazing (i.e. all ponds except those in hunting reserves are grazed). The phosphorus content of the sediment was negatively correlated with the silt content and positively correlated with the soil conductivity, positively with most human uses (except recreation and 'no use', which showed a negative correlation). The maximum water depth was not correlated with any other variable. The silt content of sediment was negatively correlated with the API index, with grazing and drainage; it was positively correlated with 'no use'. The surface area of the ponds was positively correlated with the API and with the variables 'drainage' and 'culture'. It was negatively correlated with the density of ponds in a 300-m circle. The ponds without use had higher organic matter content and total nitrogen in sediment, but lower phosphorus. Drained ponds had a higher pH and higher phosphorus (mostly agricultural ponds) along with larger surface area and higher API. Cultivated and urbanised ponds also had higher phosphorus.

Pond-characteristic species

Using forward-selection RDA, maximum water depth, pond surface, conductivity and silt content of the soil were identified as the most important local factors for the pond-characteristic species community. The most important regional factors were the density of ponds in 300-m and 1500-m radii. Also, the API

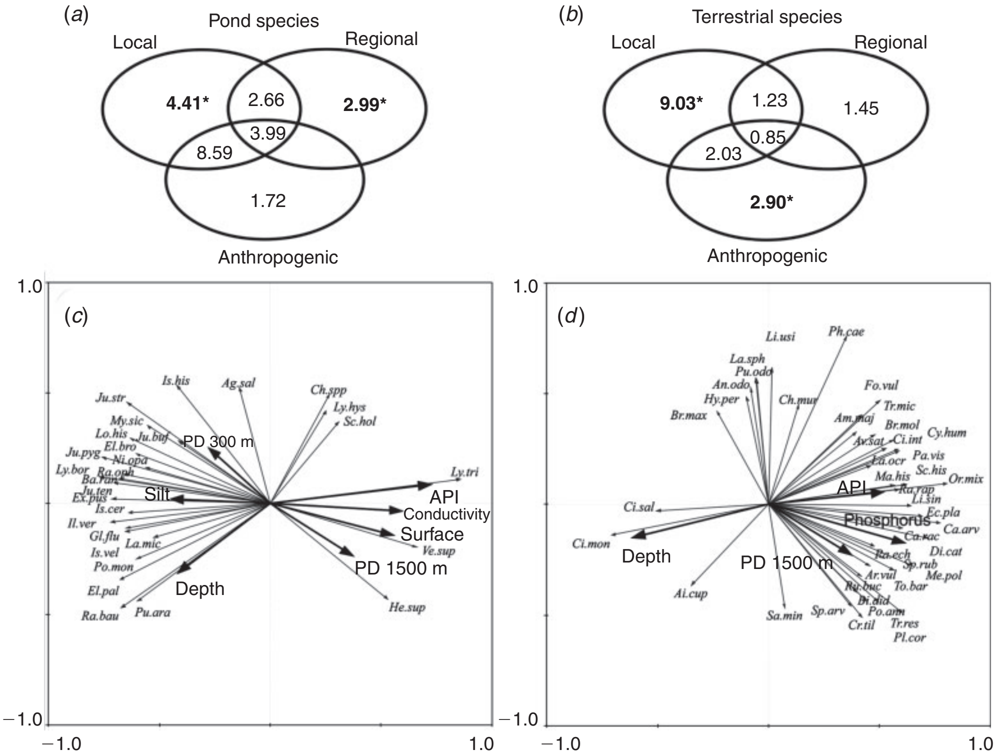

Fig. 2. Above: Variation partitioning (% explained variation based on adjusted R^2) of the plant data matrix (pond (*a*) and terrestrial (*b*) species) for the significant local, regional and anthropogenic factors. The figures in the main circles indicate the percentage of variance explained by individual factors; figures in the overlay of circles indicate the percentage of common variance explained; significant values ($P < 0.05$) are in bold and with an asterisk. Below: Ordination plots of PCA illustrating the relationship between plant community structure for pond species (*c*) and terrestrial (*d*) species and significant local, regional and anthropogenic factors, plotted as supplementary variables. API, anthropogenic pressure index; CD, conductivity; PD, pond density within a given radius. Only taxa for which more than 21% of the variation is explained by the explanatory variables are shown. For the abbreviations of species names, see Appendix 2.

had a significant effect on the species composition of the community. Together, these factors explained 24.36% of the total variance in the community species composition ($F = 2.40$, $P = 0.005$). When partitioning the variation (Fig. 2*a*), local factors explained the largest part of the unique variation (4.41%) ($F = 1.41$, $P = 0.015$), followed by regional factors (2.99%) ($F = 1.51$, $P = 0.032$) and the API (1.72%) ($F = 1.57$, $P = 0.064$). Most of the explained variation, however, is shared between local and anthropogenic factors (8.59%). On the PCA graph (Fig. 2*c*) we can distinguish a group of species (e.g. *Ranunculus baudotii*, *Eleocharis palustris*, *Exaculum pusillum*, *Illecebrum verticillatum* and *Glyceria fluitans*) that were positively influenced by the water depth, the silt content in the soil and the density of ponds within 300 m. These species are negatively related to the API, the soil conductivity, pond surface area and the density of ponds in a 1500-m radius. These species are dominant in or exclusive to the deepest ponds located in forested areas with low anthropogenic impact. A second group is composed of postinundation species (e.g. *Verbena supina*, *Lythrum tribracteatum* and *Heliotropium supinum*) favoured by anthropogenic activities, soil conductivity, pond density and low water depth. These species were found mostly or even exclusively (*L. tribracteatum*) in large shallow ponds in agricultural areas.

The number of pond-characteristic species per pond was positively correlated with the maximum water depth and the silt content of sediment, but negatively correlated with the soil conductivity, pond surface and the API (Table 2). However, it showed no significant correlation with pond density. The number and abundance of rare species were negatively correlated with the phosphorus content of sediment (Rho $= -0.646$, $P < 0.0001$, and Rho $= -0.609$, $P = 0.0002$, respectively) and with the API (Rho $= -0.592$, $P = 0.0004$, and Rho $= -0.687$, $P < 0.0001$, respectively). The abundance of rare species was also negatively correlated with the soil conductivity (Rho $=$ -0.418, $P = 0.0173$).

Terrestrial species

The local variables selected by forward-selection RDA were maximum water depth and the amount of phosphorus in the soil. The only significant regional factor was the density of ponds in a radius of 1500 m. The API also had a significant effect on the composition of the community of terrestrial species. Together, these factors explained 17.49% of the total variability in

Table 2. Spearman Rank correlations (*R*) between the number of pond species and terrestrial species with important local, regional and anthropogenic factors

Silt %, silt content of sediment; PD 300 m, pond density within 300 m radius; PD 1500 m, pond density within 1500 m radius; API, anthropogenic pressure impact; P_2O_5, phosphorus content of sediment; n.s., not significant ($P > 0.05$) ; *, $P \leq 0.05$; **, $P < 0.01$

	Factor	*R*	*P*
Pond species			
Local	Depth	0.368	*
	Conductivity	−0.397	*
	Silt %	0.357	*
	Surface	−0.440	**
Regional	PD 300 m	0.122	n.s.
	PD 1500 m	−0.279	n.s.
Anthropogenic	API	−0.596	**
Terrestrial species			
Local	Depth	−0.382	*
	P_2O_5	0.337	*
Regional	PD 1500 m	0.083	n.s.
Anthropogenic	API	0.253	n.s.

community composition ($F = 2.59$, $P = 0.005$). Variation partitioning showed that local factors alone explained most of the variability (9.03%) ($F = 2.58$, $P = 0.005$), followed by the anthropogenic factor (2.90%) ($F = 1.98$, $P = 0.005$) and, finally, the regional factor, which was not significant (1.45%) ($F = 1.49$, $P = 0.051$) (Fig. 2*b*). The shared variation was much smaller (4.11%) than for the pond species. The PCA graph (Fig. 2*d*) shows a group of species positively related with human activities and high levels of phosphorus in the soil, but negatively related with water depth (e.g. *Cladanthus mixtus*, *Scolymus hispanicus*, *Medicago polymorpha* and *Diplotaxis catholica*). These species (often weeds found in agricultural fields) are dominant or exclusive to shallow ponds located in agricultural areas. A second group consists of a small number of species in forested areas (e.g. *Cistus salviifolius*, *Cistus monspeliensis* and *Aira cupaniana*) that tolerate high water depths but are negatively impacted by human activities and high levels of phosphorus in the soil.

The number of terrestrial species per pond was negatively correlated with water depth and positively correlated with phosphorus levels in the soil (Table 2). No significant correlations were found between the richness of terrestrial species and regional or anthropogenic factors.

Effect of different land uses

The RDA used to determine the impact of the different land uses explained 28.6% of the total variation in the assemblage of the pond-characteristic species ($F = 2.68$, $P = 0.005$). The PCA graph shows that recreation activities have a rather low impact on the species composition of the community (Fig. 3). This was confirmed by the fact that no significant difference was found in species richness or abundance of rare and pond species between ponds used or not used for recreational activities (Table 3). Grazing had a weak effect on the plant community of the ponds (Fig. 3), resulting in a significant reduction of both species richness and abundance of rare and pond species (Table 3).

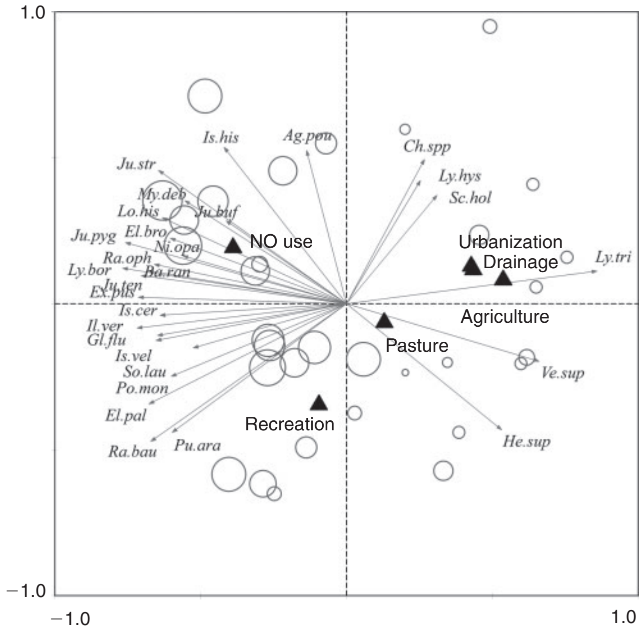

Fig. 3. Ordination plot of PCA illustrating the relations between pond-characteristic species composition and the most important uses of the temporary ponds (pasture, recreation, urbanisation, agriculture, drainage) plotted as supplementary variables. Only species for which 21% of the variance is explained by these factors have been shown. The size of the 32 circles is correlated with the number of pond-characteristic species. For the abbreviations of species names, see Appendix 2.

Grazed ponds had, on average, five characteristic pond species less than ungrazed ponds. Urbanisation, drainage and cultivation had strong impacts on community composition (Fig. 3). They reduced the richness and abundance of rare and pond species by, on average, seven species for cultivation, six species for drainage and five species for urbanisation (Table 3).

Discussion

The plant communities of the 32 temporary ponds sampled in this study were very rich (regional diversity of 200 species), with 36% of the species being pond-characteristic species, eight of which are considered rare for Morocco. Annual species dominate the communities (65%), reflecting their adaptation to the fluctuating, sometimes unpredictable, ecological conditions (mainly hydrology) imposed in this habitat. These constraints favour colonisation by species that invest more in sexual reproduction than in vegetative development (Grime 1985; Warwick and Brock 2003). The cyclical nature of these habitats (alternation of flooded and dry phases) also favours the coexistence of numerous species with short life cycles adapted to the different phases of the cycle (aquatic, amphibian and terrestrial), which, in turn, explains the high richness of these systems (Médail *et al.* 1998; Rhazi *et al.* 2006).

Factors that regulate plant community composition

Plant community composition in the ponds is influenced by a combination of local (hydrology, silt content, soluble ions content and phosphorus content of the soil), regional (pond

Table 3. Analysis of variance (ANOVA) comparing the impact of frequent land uses (presence/absence; d.f. = 1) within ponds on the richness and abundance of plant species (pond species and rare species)

s.d., standard deviation; n.s., not significant; *, $P \leq 0.05$; **, $P < 0.01$; ***, $P < 0.001$

	Pond species				Rare species			
	F	P	Mean ± s.d.		F	P	Mean ± s.d.	
			Absence	Presence			Absence	Presence
Richness								
Recreation	0.76	n.s.	26.71 ± 5.52	28.50 ± 4.66	0.11	n.s.	2.39 ± 1.81	2.50 ± 2.08
Pasture	7.29	**	31.00 ± 5.60	25.58 ± 4.68	10.89	***	4.00 ± 1.60	1.88 ± 1.57
Agriculture	16.18	***	28.75 ± 5.01	21.50 ± 1.06	12.11	***	2.96 ± 1.71	0.75 ± 0.89
Urbanisation	3.41	*	27.67 ± 5.46	23.00 ± 2.92	5.63	*	2.70 ± 1.79	0.80 ± 0.84
Drainage	9.51	**	28.57 ± 5.31	22.78 ± 2.82	9.65	***	2.96 ± 1.80	1.00 ± 0.87
Abundance								
Recreation	0.76	n.s.	66.21 ± 18.82	66.75 ± 8.25	0.19	n.s.	7.10 ± 6.00	5.75 ± 4.79
Pasture	18.97	**	85.25 ± 16.82	59.96 ± 13.11	16.79	***	12.88 ± 6.49	4.96 ± 4.05
Agriculture	24.76	***	73.00 ± 15.05	46.13 ± 5.67	12.92	***	8.75 ± 5.56	1.50 ± 1.77
Urbanisation	4.07	*	69.07 ± 17.11	51.20 ± 14.20	4.79	*	7.85 ± 5.84	2.00 ± 2.00
Drainage	10.17	**	72.04 ± 16.44	51.56 ± 11.78	8.93	***	8.65 ± 5.90	2.56 ± 2.30

density in the surrounding area) and anthropogenic (API) factors. Nevertheless, local factors seem to play the most important role for both pond-characteristic species (Fig. 2*a*) and terrestrial species (Fig. 2*b*), as was also shown in other studies on zooplankton in small aquatic systems (Vanschoenwinkel *et al.* 2008; Waterkeyn *et al.* 2008; Nhiwatiwa *et al.* 2011) and in particular for plant communities in ponds (Lathrop 1976; Koning 2005).

Hydrology is a key factor shaping plant communities in temporary ponds (e.g. Bauder 2000). The presence of species therefore depends on their life-history traits and their tolerance to hydrological stress and desiccation (Lavorel and Garnier 2002; Rhazi *et al.* 2009*a*, 2009*b*). Inundation plays a dominant role as an environmental filter by reducing terrestrial species and favouring the recruitment of aquatic species (Middleton 1999). In our study, maximum depth was an important explanatory variable, favouring pond-characteristic species and, conversely, excluding terrestrial species (Fig. 2*c*, *d*). Other important local factors were soil silt content (positively related with the abundance of pond-characteristic species) and the soluble ions and phosphorus content of sediment (positively related with the abundance of the terrestrial species). The silt content of sediment was negatively correlated with both phosphorus and soluble ion content (conductivity) of sediment (which are also correlated). Because agriculture is usually established on richer soils, the effect of these three factors cannot clearly be separated in this study and result probably from both natural characteristics of soils and impacts from anthropogenic uses. Soil phosphorus content characterises different trophic levels, which can result from both soil characteristics and nutrient input through sewage or leakage from surrounding agricultural areas. Similarly, in a poorly buffered environment (low Ca concentration), increased content of soluble ions can also result both from nutrient inputs from cultivated areas or cattle manure (Croel and Kneitel 2011).

Few studies have addressed the impact of eutrophication on the vegetation of temporary ponds. Our results suggest an impact of the nutrient levels on the species composition of the plant community of the ponds. Most of the pond-characteristic species (except *H. supinum*, *L. tribracteatum* and *V. supina*) (Fig. 2*a*) and the most threatened species in Mediterranean temporary ponds are oligotrophic species that are negatively impacted by high nutrient levels (Daoud-Bouattour *et al.* 2011). In California vernal pools, nutrient addition by cattle waste significantly altered plant communities (Kneitel and Lessin 2010; Croel and Kneitel 2011). In these pools, nutrient addition led to a decrease of species richness and cover of plants of the terrestrial phase resulting from extensive growth of filamentous algae forming thick mats on the soil surface (Kneitel and Lessin 2010; Croel and Kneitel 2011). In the ponds we studied, filamentous algae were of only marginal importance. In temporary flooded habitats, the low depth of water probably reduces the effects of light attenuation on the aquatic phase, lowering the negative impact of algal growth on vascular plants. Other processes, such as competition, are expected to influence the effects of eutrophication in pools (Weigelt *et al.* 2002; Rhazi *et al.* 2009*b*), but more research is needed to acquire a better understanding of the impact of eutrophication on pond ecosystems.

Pond density in the surrounding area also significantly influenced plant species composition, as was also found by Rhazi *et al.* (2012). This suggests that dispersal dynamics, which are linked to interpond distances, may influence the plant communities in ponds. Effective dispersal may be promoted by several vectors, such as wind and animals. Nevertheless, the wind speed in the Benslimane region is relatively low (average of 15 km h^{-1}), which is further attenuated by the cork oak forests that dominate the study area. The role of waterbirds may also be limited because of their low numbers visiting ponds in the region. Large mammals are known for their high dispersal capacity (Heinken *et al.* 2006; Vanschoenwinkel *et al.* 2008). The large nomadic herds of cattle, sheep and goats that graze, drink and wallow freely in the ponds probably transport sediment (containing high numbers of dormant stages) from pond to pond. Also, a fairly large wild boar population is present in the forested part of the study area (M. Chakar, pers. comm.). The movements of these vectors between ponds are important to guarantee dispersal dynamics and maintain metapopulations and communities at the landscape scale. The ongoing destruction of ponds in Morocco (0.5% per year: Rhazi *et al.* 2012) due to urbanisation and agriculture can disturb the metacommunity dynamics through reduced efficient dispersal and thus cause isolated ponds to become more vulnerable.

The common variability between local, regional and anthropogenic factors found in the results of the variation partitioning underlines the correlations between the variables involved. The relatively low weight of regional factors could reflect the lower number of variables used in the analyses. However, this is unlikely as this effect is taken into consideration in the analyses (R^2 adjusted). Furthermore, additional regional factors would likely be correlated with local factors that have more direct impact on species. The considerable amount of common variability found between local and anthropogenic factors for pond-characteristic species probably results from two processes. First, some uses depend on local factors (e.g. agriculture on more productive soils). Second, it is mostly through modifications of local physical (e.g. hydroperiod) and chemical (e.g. water and soil quality) factors that human activities can influence the plant communities in ponds. The sediment in grazed ponds showed lower content of organic matter and total nitrogen than in ungrazed ones (in hunting reserves). This difference is consistent with the greater accumulation of plant material in ungrazed ponds. Grazing may favour the pond ecosystem by impacting the hydrological functioning. Defoliation by grazers can reduce water losses through evapotranspiration, thus increasing the duration of the flooded phase (Bremer *et al.* 2001; Pyke and Marty 2005). The total measured anthropogenic impact remains, however, relatively limited. The species richness of the studied ponds and the exceptionally good hydrological conditions in 2009 probably masked, in part, the true anthropogenic impact, which may be more pronounced in dryer years.

Effect of different land uses

The numbers of pond-characteristic species and of rare species were negatively correlated with the API, although a few pond-characteristic species (e.g. *L. tribracteatum*, *V. supina, H. supinum*) seem to be resistant to human activities. With the exception of recreation, all other activities (grazing, drainage, agriculture and partial urbanisation) significantly reduced the number of pond species. The impacts of the different human activities in the ponds probably depend on the nature of the disturbances linked to the activity (Bisigato *et al.* 2009) and the life-history traits of the different species (Grime 1985; Fenner 2000).

Plowing for agriculture can lead to the destruction and burying of seeds (Devictor *et al.* 2007), inhibiting germination. This is especially important for small seeds (typical for pond species such as *Elatine brochonii* and *E. alsinastrum*) since their energy reserve does not allow them to break through thick layers of sediments and they are more light dependent for germination (Milberg *et al.* 2000). Additionally, agriculture can lead to eutrophication of the pond due to the use of fertilisers (agriculture was indeed correlated with the phosphorus content of sediment: Appendix 1) and favours ruderal plants (e.g. *Diplotaxis catholica*, *Raphanus raphanistrum*, *Scolymus hispanicus*) (Anderson and Vondracek 1999; Rhazi *et al.* 2001, 2006). Nevertheless, certain pond-characteristic species, such as *Damasonium stellatum*, *L. tribracteatum* and *V. supina*, seem to be more abundant in cultured ponds (Fig. 3). It is possible that homogenisation of their seed banks (and therefore breaking dormancy of buried seeds when they are surfacing) through plowing can allow for an annual recruitment (Devictor *et al.* 2007). Additionaly, their life-history traits, such as their annual life-cycle, the production of persistant seed banks (e.g. *D. stellatum*) and late phenology (e.g. *L. tribracteatum*, *V. supina*) may allow them to reduce competition, favouring their recruitment.

Drainage can modify the hydrological regime of ponds, which is a key factor determining their ecological functioning. Drainage of the ponds was correlated with all uses except recreation (Appendix 1). The species richness and abundance of pond-characteristic species was positively related to water depth. Indeed, a delayed or shorter inundation due to drainage can affect the reproduction of most aquatic species (e.g. Charophyta, *Callitriche*, *Myriophyllum*) (Bonis *et al.* 1993) and favour the recruitment of species adapted to the terrestrial phase (e.g. *Raphanus raphanistrum* and *Scolymus hispanicus* in our study).

Grazing significantly reduced the richness and abundance of pond-characteristic species, such as *Elatine alsinastrum*, *E. brochonii* and *Nitella opaca*. Grazing influences the ecology of temporary wetlands through several mechanisms, such as phytomass removal, trampling and the alteration of nutrients dynamics (Robins and Vollmar 2002) and hydrology (Pyke and Marty 2005). In our study, most pond-characteristic species are very palatable and thus are directly impacted by grazing. Some species seem to resist grazing, such as *D. stellatum*, *H. supinum*, *L. tribracteatum* and *R. baudotii*. These species possess traits that allow them to escape or reduce the impact of grazing (Noy-Meir *et al.* 1989), such as having a short life-cycle (e.g. *L. tribracteatum*, *D. stellatum*), late phenology (e.g. *L. tribracteatum*, *H. supinum*) and morphological plasticity (e.g. *R. baudotii*) or traits reducing grazing pressure, such as prostrate growth form (e.g. *H. supinum*, *V. supina*), content in alkaloids (e.g. *Ranunculus spp.*, *V. supina*) and density of hairs (e.g. *H. supinum*). Indirect impacts of the presence of cattle were mediated by the altered quality of water (higher turbidity due to trampling and eutrophication due to manure) and sediment (decreased levels of nitrogen and organic matter in the sediment). Nevertheless, grazing can also have a positive impact on the conservation of temporary pond biota, notably by reducing the cover of dominant species and thus decreasing the intensity of competition (Robins and Vollmar 2002; Marty 2005).

Conclusions

The composition and species richness of plant communities in the temporary ponds of Benslimane are the result of a combination of local, regional and anthropogenic factors. As predicted, local factors, such as hydrology and water and soil quality, play a dominant role, but there are important interactions with regional and anthropogenic factors. The importance of pond density also suggests an influence of dispersal processes, which sustains metacommunity dynamics. A reduction in pond density in the landscape due to the destruction of ponds for urban or agricultural purposes can disrupt dispersal dynamics. Anthropogenic pressure, in the form of different activities performed in and around the ponds by the local population, influences the plant communities, mostly through the modification of local factors such as shortened inundations or raised nutrient levels. Drainage, agriculture, grazing, and partial urbanisation significantly reduced plant species richness and altered community composition. This is particularly true for the most remarkable species which are dependent on oligotrophic conditions. However, certain human activities (recreation and, to a lesser extent, grazing) seem to be compatible with conserving a high floristic richness and rare species. In the context of the current demographic development of Morocco, the threats to temporary ponds and their unique communities are alarming in the short term. The main challenge for the conservation of these habitats is to rapidly reach a compromise between the needs of the local populations and biodiversity conservation through sustainable development. Networks of ponds on the most oligotrophic soils should be the primary focus for conserving the rich flora of Mediterranean temporary ponds.

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Appendix 1. Mean and standard deviation (St.de) of each factor and matrix of correlations between the factors used in the analyses

Depth, maximum water depth; pH, pH of sediment; OM, organic content of sediment; Nitrogen, total nitrogen content of sediment; P_2O_5, phosphorus content of sediment; Cd, soluble ions content in sediment; Clay, clay content of sediment; Silt, silt content of sediment; Sand, sand content of sediment; Surface, surface area of the pond; API, anthropogenic pressure index; PD 0.3 km, pond density within 0.3 km; PD 1.5 km, pond density within 1.5 km; $n = 32$; $P < 0.05$ for $R > 0.3494$; $P < 0.01$ for $R > 0.4487$ For more details, see Methods

	Mean	St.de	Depth	pH	OM	Nitrogen	P_2O_5	Cd	Clay	Silt	Sand	Surface	API	No use	Grazing	Recreation	Agriculture	Urbanisation	Drainage	PD 0.3 km	PD 1.5 km
Depth (cm)	46.41	22.64	1.000																		
pH	6.12	0.46	0.064	1.000																	
OM (%)	3.27	1.40	0.163	−0.139	1.000																
Nitrogen (g/kg)	1.86	0.72	0.024	−0.049	**0.908**	1.000															
P_2O_5 (g/kg)	51.18	40.73	−0.184	0.246	−0.289	0.002	1.000														
Cd (mS/cm)	323.99	438.73	−0.230	0.178	0.073	0.319	**0.484**	1.000													
Clay (%)	28.76	9.47	0.033	−0.140	**0.367**	**0.412**	−0.083	**0.381**	1.000												
Silt (%)	23.61	12.73	0.131	−0.006	0.339	0.139	**−0.580**	−0.304	−0.244	1.000											
Sand (%)	28.00	11.90	0.162	−0.060	0.107	−0.111	−0.305	−0.199	**−0.518**	0.313	1.000										
Surface (ha)	2.16	2.01	0.029	0.337	0.162	0.261	0.325	**0.459**	0.200	−0.096	−0.109	1.000									
API	5.86	5.34	−0.176	0.266	−0.318	−0.134	**0.593**	**0.556**	0.131	**−0.593**	−0.191	**0.528**	1.000								
No use	0.25	0.44	0.174	−0.202	**0.575**	**0.375**	**−0.495**	−0.317	0.009	**0.666**	0.252	−0.224	**−0.644**	1.000							
Grazing	0.75	0.44	−0.174	0.202	**−0.575**	**−0.375**	**0.495**	0.317	−0.009	**−0.666**	−0.252	0.224	**0.644**	**−1.000**	1.000						
Recreation	0.13	0.34	0.269	−0.172	−0.090	−0.141	**−0.354**	−0.212	−0.083	0.069	0.120	0.067	−0.044	−0.218	0.218	1.000					
Agriculture	0.25	0.44	−0.166	0.078	0.028	0.164	**0.460**	**0.712**	**0.393**	−0.349	−0.196	**0.564**	**0.785**	−0.333	0.333	−0.218	1.000				
Urbanisation	0.16	0.37	−0.240	−0.012	−0.235	−0.131	**0.410**	0.245	−0.062	−0.347	−0.192	**0.434**	**0.699**	−0.248	0.248	−0.163	**0.547**	1.000			
Drainage	0.28	0.46	−0.102	**0.428**	−0.098	0.065	**0.592**	**0.497**	0.210	**−0.375**	−0.175	**0.553**	**0.705**	**−0.361**	**0.361**	−0.236	**0.602**	0.305	1.000		
PD 0.3 km	0.78	1.01	−0.095	−0.071	−0.076	0.032	0.242	−0.077	−0.221	−0.055	−0.013	**−0.403**	**−0.228**	−0.018	0.018	−0.107	−0.309	−0.339	−0.142	1.000	
PD 1.5 km	5.19	3.35	**−0.371**	0.056	−0.217	0.035	**0.375**	**0.281**	−0.002	−0.289	−0.156	**0.059**	**0.095**	**−0.493**	**0.493**	0.007	0.099	−0.103	0.175	0.348	1.000

Appendix 2. Abbreviations and categories of species names used in the figures

Category: P, pond; T, terrestrial

Species	Abbreviation	Category
Agrostis pourretii	*Ag.pou*	P
Aira cupaniana	*Ai.cup*	T
Ammi majus	*Am.maj*	T
Anthoxantum odoratum	*An.odo*	T
Avena sativa	*Av.sat*	T
Baldellia ranunculoides	*Ba.ran*	P
Biscutella didyma	*Bi.did*	T
Briza maxima	*Br.max*	T
Bromus mollis	*Br.mol*	T
Calendula arvensis	*Ca.arv*	T
Carlina racemosa	*Ca.rac*	T
Chara sp	*Ch.spp*	P
Cichorium intybus	*Ci.int*	T
Cistus monspeliensis	*Ci.mon*	T
Cistus salviifolius	*Ci.sal*	T
Cladanthus mixtus	*Cl.mix*	T
Crassula tillaea	*Cr.til*	T
Cynara humilis	*Cy.hum*	T
Diplotaxis catholica	*Di.cat*	T
Echium plantagineum	*Ec.pla*	T
Elatine brochonii	*El.bro*	P
Eleocharis palustris	*El.pal*	P
Exaculum pusillum	*Ex.pus*	P
Foeniculum vulgare	*Fo.vul*	T
Glyceria fluitans	*Gl.flu*	P
Heliotropium supinum	*He.sup*	P
Hypericum perfoliatum	*Hy.per*	T
Illecebrum verticillatum	*Il.ver*	P
Isoetes histrix	*Is.his*	P
Isoetes velata	*Is.vel*	P
Isolepis cernua	*Is.cer*	P
Juncus bufonius	*Ju.buf*	P
Juncus pygmaeus	*Ju.pyg*	P
Juncus striatus	*Ju.str*	P
Juncus tenageia	*Ju.ten*	P
Lathyrus ochrus	*La.och*	T
Lathyrus sphaericus	*La.sph*	T
Limonium sinuatum	*Li.sin*	T
Linum usitatissimum	*Li.usi*	T
Lotus hispidus	*Lo.his*	P
Lythrum borysthenicum	*Ly.bor*	P
Lythrum hyssopifolia	*Ly.hys*	P
Lythrum tribracteatum	*Ly.tri*	P
Malva hispanica	*Ma.his*	T
Medicago polymorpha	*Me.pol*	T
Myosotis debilis	*My.deb*	P
Nitella opaca	*Ni.opa*	P
Paronychia echinata	*Pa.ech*	T
Phalaris caerulescens	*Ph.cae*	T
Plantago coronopus	*Pl.cor*	T
Poa annua	*Po.ann*	T
Polypogon monspeliensis	*Po.mon*	P
Pulicaria arabica	*Pu.ara*	P
Pulicaria odora	*Pu.odo*	T
Ranunculus baudotii	*Ra.bau*	P
Ranunculus ophioglossifolius	*Ra.oph*	P
Raphanus raphanistrum	*Ra.rap*	T

(*Continued*)

Appendix 2. (Continued)

Species	Abbreviation	Category
Rumex bucephalophorus	*Ru.buc*	T
Sanguisorba minor	*Sa.min*	T
Scirpoides holoschoenus	*Sc.hol*	P
Scolymus hispanicus	*Sc.his*	T
Solenopsis laurentia	*So.lau*	P
Spergula arvense	*Sp.arv*	T
Spergularia rubra	*Sp.rub*	T
Tolpis barbata	*To.bar*	T
Trifolium micranthum	*Tr.mic*	T
Trifolium resupinatum	*Tr.res*	T
Verbena supina	*Ve.sup*	P